Avian bioacoustics in urbanizing landscapes: relationships between urban noise and avian singing behavior.

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Abstract

Song is a defining characteristic in avian communication systems because of its role in mate attraction, territory establishment, territory defense, and habitat selection. Therefore, biologists are increasingly concerned about potential behavioral and reproductive consequences of anthropogenic noise as it creates novel acoustic environments for birds. In this study, I examine the extent to which acoustic noise in urban environments influences the song characteristics and/or singing behavior of passerines. I predicted that, in response to loud noises, birds may (1) increase singing rate and/or repetition of songs (including percent of time spent singing), and (2) adjust song characteristics such as pitch (frequency) and song length. Both of these strategies have the potential to improve signal transmission by reducing overlap of signals with ambient noise. Preliminary decibel level data were collected in four ***a priori*** environments to establish the amount of noise disturbance in relation to the type of urban area. From May – July 2006, song frequency, duration, and singing rate were measured for 42 Northern Cardinals (*Cardinalis cardinalis*) and 53 American Robins (*Turdus migratorius*) in forests located within these four increasingly louder acoustic environments (rural to residential, commercial, and highway) in central Ohio. Song characteristics were digitally measured via computerized spectrogram analysis. As predicted, frequency range was positively correlated to noise level for both species. These data suggest that anthropogenic noise may influence avian singing behavior and therefore has the potential to be a relatively novel selective force in urban areas.

Introduction

Song is a defining characteristic of avian communication systems. The role of song in mate attraction, territory establishment and defense, as well as habitat selection has been demonstrated for a wide variety of species and habitats (Thomson 1964). Though rarely studied in urban environments, the ability of the singing male to modify its song characteristics is closely related to improving his efficiency of signal transmission (Brenowitz 1982, Ryan and Brenowitz 1985, Klump 1996, Brumm and Slater 2005, Brumm 2006). This suggests that song characteristics (such as frequency, duration, and amplitude) are under selective pressure, favoring effective transmission of the song signal to the receiver (listener) (Brumm and Slabbekoorn 2005). In addition to whales (Lesage et al. 1999) and frogs (Bee et al. 2000, Lardner and bin Lakim 2002), certain avian species have been known to alter their vocal frequencies (Hultsch and Todt 1996, Manabe 1997, Slabbekoorn and Peet 2003). Evidence suggests that some animals also adjust the duration of their signals to reduce the masking effects of temporarily elevated noise (like that from a highway) (Brumm et al. 2004). Some species use an additional strategy to improve transmission efficiency by increasing their song redundancy (singing more repetitions of the same notes) (Shannon and Weaver 1949, Potash 1972, Lengagne et al. 1999).

Although birds are exposed to a variety of naturally-occurring noise sources (waterfalls, etc.), biologists are increasingly concerned about potential behavioral and reproductive consequences of anthropogenic noises since they may create a novel acoustic environment for most species (Brumm and Slabbekoorn 2005). There are four recognized features of bird song that might be sufficiently flexible to accommodate such novel acoustic environments: frequency structure, amplitude (i.e., loudness), temporal structure (timing of modulations, notes, and syllables within vocalizations), and timing of vocal delivery (repetition rate of vocalizations, diel patterns) (Patricelli and Blickely 2006). Urban anthropogenic noise sources—such as traffic, industry, and airports—introduce sounds with amplitudes, frequencies, and temporal patterns that are different than those produced by most natural sound sources. This may both eliminate gaps that could be used for signal transmission and produce decibel levels that could mask bird song (Brumm 2006, Slabbekoorn et al. 2007). Although most anthropogenic noise is of relatively low frequencies (usually <2000 Hz), masking effects of such low-pitched ambient noise have been shown to spread upward and compete with frequencies higher than 2000 Hz. This masking effect further decreases the frequency range available to birds that had otherwise been absent of same-frequency interruptions (Moore 1997). A few studies have found that birds can adapt to urban noise (Brumm and Todt 2002, Slabbekoorn and Peet 2003, Brumm 2004a, Brumm 2004b, Wood and Yezerinac 2006, Slabbekoorn and den Boer-Visser 2006). Birds may increase the low frequency of their song, increase their singing rate (Fernandez-Juricic et al. 2005), and alter the high-frequency pitches of their songs (Slabbekoorn and Smith 2002a). While these studies show that birds may have the capacity to respond to novel acoustic environments, biologists have a poor understanding of how individuals in urban areas use this capacity to modify their songs in order to increase signal transmission (Brumm 2006).

In this study, I examined the extent to which acoustic noise in urban environments was related to the song characteristics and/or singing behavior of songbirds. I predicted that, in response to loud noises, birds may (1) increase singing rate and/or repetition of songs (including percent of time spent singing), and (2) adjust song characteristics such as pitch (frequency) and song length. All of these strategies have the potential to improve signal transmission by reducing overlap of signals with ambient noise. Because most urban anthropogenic noise is below 2000 Hz (Warren 2006, Wood and Yezerinac 2006), I predicted that faster singing rates, higher frequencies (for ***short-distance*** transmission), and longer songs would be favored in most urban environments. By singing more frequently within the same time interval, an individual would have a greater chance of transmitting the signal. By raising song frequency, birds might produce notes that are less likely to be masked by comparatively low frequency urban noise. This strategy would be most beneficial for transmission to local conspecifics due to the quicker attenuation of higher frequencies over distance as compared to lower frequencies (Larom 2002). Longer songs would presumably increase the likelihood that a larger portion of the song will not be interrupted.

Methods

Focal species

The American Robin (*Turdus migratorius*) and Northern Cardinal (*Cardinalis cardinalis*) were selected as focal species because they are common breeding birds in rural and urban landscapes in Ohio. Both species are easily identifiable, have obvious songs that can be readily discriminated from their call notes, and sing more than one note type (creating a potentially flexible repertoire) (Kroodsma 2005). In addition, cardinals are an appropriate focal species because (1) their songs are typically pure-toned and (2) the right side of the syrinx is possibly specialized for high-frequency notes that are not usually utilized (Halkin and Linville 1999). Similarly, robins are especially appropriate for this study because (1) their whisper syllables have high propensity for reaching above their normal frequency range and (2) they regularly use specialized song types with high frequency notes (Sallabanks and James 1999). The timing of this study coincided with the peak breeding season for both species. Most breeding pairs establish territories and acquire mates by late March – early April and make multiple nesting attempts throughout the summer. Because habitats in fragmented central Ohio are subject to high rates of nest predation (A.D. Rodewald, unpublished data), the nesting stages of individuals was asynchronous with birds ranging from building nests to brooding nestlings.

Study areas and location selection

In an attempt to reduce potential confounding effects of local habitat conditions on bird quality and singing behavior, sampling locations were limited to wooded habitats within four *a priori* acoustic environments: (1) major highway (>4 lane divided highway), (2) commercial district (where >50% of a 1-mile stretch of the nearest road bordered by commercial development), (3) residential (2-lane roads bordered by single-family homes), and (4) rural (landscapes dominated by agricultural land uses). These acoustic environments were expected to differ both in ambient sound intensity (decibels) and in temporal patterns of noise (e.g. rush hour).

Field locations were opportunistically selected by driving along roads and visiting forests of the four acoustic environments as they were encountered. Sampling was conducted at these locations between 0600 and 1000 from May-June of 2006. In total, sampling locations included 11 highway, 11 commercial, 8 residential, and 11 rural sites.

To the greatest extent possible, I sampled within multiple types of acoustic environments each morning and rotated the visitation order of them to prevent any systematic bias. Because traffic patterns, and hence traffic noise, differ dramatically between weekends and weekdays, sampling was limited to non-holiday weekdays.

During each sampling visit, I located focal individuals opportunistically. Because subjects were not banded, the likelihood of resampling individuals was reduced using the following rule: a conspecific was only recorded if it was detected >200 m away from the previously recorded individual during the same morning. The only exception to this rule was when a second individual was detected during the initial recording (i.e. it was known to be a different individual based on countersinging) and was ≥75m away. Multiple recordings for the same species at a single sampling location only occurred during a single morning's sampling period.

Songs were recorded using a Marantz PMD 670 digital recorder and an Audio-Technica 815a shotgun directional microphone. Factory presets were used on the Marantz digital recorder: sounds were sampled at 44.1 kHz with a bit rate of 32 kbps, and saved as mono .mp3 files. All recordings were collected <20m from the focal individual with the microphone directed towards the focal bird (mean distance = 12.7 m + 1.31 SD). Focal birds were recorded for either a minimum of 10 songs or a total of five minutes. A series of post-recording measurements were collected to describe the position of the focal individual, including horizontal distance from microphone to bird (m), height of bird (m), orientation of bird relative to microphone (with 0 degrees indicating bird directly facing microphone), substrate type of singing perch, bird's position on substrate (inner, middle, outer), and any obstructions (e.g. leaves or branches) between the microphone and the bird.

In cases when the focal individual moved during the recording period, recording continued provided it moved <15 m, and a second set of measurements describing the location of the bird were collected. Immediately after recording each focal individual, four sound meter measurements were collected at 30-sec intervals for a 2-min period with the sound meter facing in the direction of the nearest roadway. Simultaneously, I surveyed the number of conspecific individuals detected either visually or aurally during 0-2 minutes and 2-5 minutes. These detections were grouped into 3 distance categories of 0-25 m, 25-50 m, and 50-75 m.

The following habitat characteristics were measured within a 25-m radius area centered on the focal bird's location when recorded: number and percent cover of deciduous trees (≥ 8 cm dbh), number and percent cover of coniferous trees (≥ 8 cm dbh), number of snags, percent cover of woody shrubs and saplings, herbaceous vegetation, lawn, pavement, water, and number and percent cover of buildings. Percent cover was estimated using the scale developed by Prodon and Lebreton (1981). Average canopy height and height of the substrate where the focal individual was located were estimated by using a pencil to visually rotate the plant tips 90 degrees onto the ground and then measuring that ground distance with a meter tape (Fernandez-Juricic et al. 2005). The coordinates of the locations were also recorded using a Garmin model GPS unit.

After recording, the .mp3 files on the Marantz were transferred to a PC and converted to PCM.wav files using CDex software (v. 1.51) at a sample rate of 44 kHz and a sample size of 16 bits. On-screen spectrograms were then generated in Raven (Chariff et al. 1995) using a Hanning type window, an FFT (Fast Fourier Transform) size of 512, and a 50% time grid overlap. Visual contrast was adjusted for each spectrogram to give the song maximum visibility. Individual songs were manually selected using an on-screen cursor. Robin frequency resolution was 34.4 Hz and time increments were in 5 ms. Cardinal frequency resolution was 43.0 Hz and time increments were in 12 ms.

A song was considered to be a series of notes, usually more than one type, sung in succession to create a recognizable sequence or pattern (British Ornithologists' Union 1964). I defined a "song" differently for each focal species. A single robin song is a series of phrases (including "hissely" and buzzed phrases) separated by a gap visually evident to be at least twice as long as the gaps between phrases of the song (Kroodsma 2005). A single cardinal song is a bout of pure whistles (sweeping either up or down in frequency) in rapid succession (within fractions of seconds of each other) and is separated from other songs by gaps at least 3 times as long as those between the pure whistles (Kroodsma 2005). Parameters measured for each song were high (maximum) frequency, low (minimum) frequency, max (peak) frequency, start time, end time, delta time, and delta frequency. High (max) and low (min) frequency are the upper and lower frequency limits of each song and were dependant upon the manual on-screen cursor selection. Max (peak) frequency is the loudest frequency within the song, representing the pitch that the bird produced at the greatest amplitude in relation to the other pitches. Peak frequency was automatically calculated by the Raven program, as were delta time (length of each song) and delta frequency (the range of pitches of each song). A coefficient of variation was also calculated for high, low, and maximum frequencies to quantify variation in frequencies used by individual birds.

While several laboratory studies have shown that birds respond to noise by increasing the amplitude of their song through what is known as the Lombard effect (Potash 1972, Sinnott et al 1975, Cynz et al 1998, Manabe et al 1998, Dooling et al 2000, Brumm and Todt 2002, Kobavasi and Okanova 2003, Lohr et al 2003, and Brumm 2004), I did not examine this song feature because accurately measuring amplitude under natural conditions is difficult (Brenowitz 1982). Although the Lombard effect is well studied in laboratory experiments (Brumm and Slabbekoorn 2005), sound pressure measurements in natural and urban habitats are problematic since they are often collected without detailed knowledge of and/or a lack of allowance for, the spectral distribution of ambient noise. Furthermore, differences in vegetation structure throughout the recording environment as well as varied distances from the focal subject, wind speed and direction, and direction of the microphone relative to the bird's beak, can affect sound pressure readings.

Peak Frequency Verification

To address the possibility that background noise in the recordings might potentially affect the peak frequency measurements generated by the computer (i.e. if the background noise contains a more prominent frequency than the song), I verified the accuracy of the recordings by comparing max frequency measurements for identical recordings with and without background noise. To do this, I randomly selected 35 songs across all acoustic environments and removed the background noise from them using SIGNAL software (Engineering Design, Berkeley CA). These samples were then reanalyzed in the Raven software. Sound Forge 4.5 (Sonic Foundry, Madison, WI) was used to isolate a segment of background noise immediately after the song to be filtered, and SIGNAL 4.0 for Windows (Engineering Design 2001) was used to subtract the data in this segment from the data in a segment containing the song. Both the isolation and data-subtraction processes used PCM.wav file format. Because all but one song yielded the exact same peak frequencies, background noise is considered to not skew the results of peak frequency measurements made by the Raven software (Table 4).

Data analysis

I used multivariate analyses of variance (MANOVA) followed by *a posteriori* univariate tests to analyze differences among the four acoustic environments in terms of (1) song characteristics (high frequency, low frequency, frequency range, peak frequency, coefficients of variation [cv] for frequencies, song length, and song rate), (2) position of the bird (distance from ground, distance from microphone, direction focal individual facing relative to the microphone, meters from the road, meters from forest edge, and any obstructions between the focal individual and the microphone), (3) weather differences (temperature, precipitation, wind speed, wind direction, percent relative humidity, and number of dogs and people present), and (4) habitat differences (number and percent cover of deciduous trees (≥ 8 cm dbh), number and percent cover of coniferous trees (≥ 8 cm dbh), number of snags, percent cover of woody shrubs and saplings, herbaceous vegetation, lawn, pavement, water, number and percent cover of buildings, average canopy height, and height of the substrate on which the focal individual was sitting). Analyses were conducted separately for each species. Differences in decibel level among the acoustic environments were tested using an analysis of variance on the mean decibel level recorded during each sampling period. Differences in the relative abundance of conspecifics were analyzed separately for robins and cardinals using an analysis of variance. All analyses were conducted using SAS Statistical Software. Because sample sizes were relatively small, an alpha level of 0.1 was chosen to indicate statistical significance.

Results

Between 3 May – 6 July 2006, songs were recorded from 42 cardinals (6 highway, 10 commercial, 17 residential, and 9 rural) and 53 robins (14 highway, 11 commercial, 10 residential, and 18 rural). Ambient noise levels of the four ***a priori*** acoustic environments differed significantly ($F_{3,90}$ = 32.43, p< 0.0001, R^2 = 0.52, Figure 1). As expected, highway environments were loudest (60.56 dB = 0.9317 SE), followed by commercial (57.52 dB = 1.164 SE), residential (53.68 dB + 0.9806 SE), and rural (47.70 dB + 0.7261 SE).

Song characteristics differed significantly among the four acoustic environments for both Northern Cardinals ($F_{24,87.61}$ = 2.16, P = 0.005) and American Robins ($F_{24,122.41}$ = 2.40, P = 0.0010). *A posteriori* univariate analysis tests show that songs of cardinals tended to have higher-pitched high frequencies ($F_{3,37}$ = 3.55, P = 0.0234), wider ranges of frequencies used in songs ($F_{3,37}$ = 2.69, P = 0.060), and lower variation in the frequencies used in songs ($F_{3,37}$ = 2.56, P = 0.0695) as acoustic environments became louder (Table 1). Songs of robins generally had higher-pitched low frequencies ($F_{3, 49}$ = 9.62, P <0.0001) and less variation in low frequencies used ($F_{3, 49}$ = 3.01, P =0.0388) in loud acoustic environments and showed marginally significant variation among acoustic environments in high frequencies ($F_{3, 49}$ = 2.40, P =0.0793) and range of frequencies used in songs ($F_{3, 49}$ =2.66, P =0.0587), though these latter two results were not related as expected to ambient noise level (Table 1).

Because habitat features did not significantly differ among the acoustic environments at locations where cardinals were recorded ($F_{27, 85.337}$ = 0.92, P = 0.5775; Table 2), differences in song characteristics of cardinals were unlikely to be caused by habitat correlates of the acoustic environments. In contrast, habitat structure surrounding recording locations of robins differed among the acoustic environments ($F_{27,123.3}$ = 2.07, P = 0.0039), in terms of percentages of herbaceous vegetation ($F_{3,50}$ = 2.46, P = 0.0738), lawn ($F_{3,50}$ = 3.44, P = 0.0237), pavement ($F_{3,50}$ = 3.37, P = 0.0255), and number of buildings ($F_{3,50}$ = 8.10, P = 0.0002).

Recording location metrics also differed among acoustic environments for cardinals ($F_{27,85.337}$ = 2.38, P = 0.0014) and robins ($F_{27,120.38}$ = 2.75, P<0.0001). Cardinals were recorded farther from road surfaces in louder environments, a pattern that largely due to obstacles (i.e. fences) adjacent to highway and commercial roadways ($F_{3,37}$ = 8.25, P = 0.0002; Table 2). Relative humidity also differed among environments ($F_{3,37}$ = 3.25, P = 0.0325), though not predictably with noise level. Recording locations for robins differed among the acoustic environments in terms of percentage of cloud cover ($F_{3,49}$ = 4.34, P = 0.0086), distance from road surfaces ($F_{3,49}$ = 10.74, P = <0.0001), temperature ($F_{3,49}$ = 2.41, P = 0.0779), and relative humidity ($F_{3,49}$ = 2.59, P = 0.0631; Table 2).

Numbers of conspecifics averaged 1.5-3.3 individuals per recording location and did not significantly differ among the acoustic environments for either cardinals ($F_{3,37}$ = 1.57, P = 0.2139) or robins ($F_{3,50}$ = 0.67, P = 0.5731).

Discussion

Song characteristics of cardinals and robins were associated with the level of anthropogenic noise. In general, songs in less noisy environments (i.e. rural and residential wooded areas) contained lower frequency notes than songs in louder wooded environments (i.e. highway and commercial habitats). These findings are consistent with frequency range shifts found in previous studies in both natural and urban acoustic environments. For example, both the Black-faced Warbler (*Abroscopus albogularis*; Narins et al 2004) and the Large-billed Leaf-warbler (*Phylloscopus magnirostris*; Dubois and Marten 1984) use high-frequency notes in song to offset acoustic masking by loud water noise (e.g. waterfalls and rushing streams). Similar shifts in song characteristics are thought to arise in environments with high levels of urban noise pollution. For example, Slabbekoorn and van Boer-Visser (2003, 2006) found that songs of Great Tits (*Parus major*) living in 10 European cities had significantly higher minimum frequencies and shorter inter-song intervals as compared to individuals living in more rural areas. Maximum frequencies used in songs also may change in response to loud environments, and cases of birds in noisy environments increasing frequencies have been reported in Europe, (Slabbekoorn and Peet 2003), California (Fernandez-Juricic 2005), and the Netherlands (Wood 2006). Shifting frequency upwards would maximize the clarity of the signal to proximate conspecifics since most of the song components at or below 2000 Hz would be masked by traffic noise (Warren 2006, Wood and Yezerinac 2006). Amplitude of urban traffic noise would logically correlate with the amount of low-frequency masking effects, causing high-frequency songs to be less effected and ergo more transmittable.

Although bioacoustic research has established patterns of association between song characteristics and anthropogenic noise, the mechanisms underlying such associations remain unclear. Associations between song and urban noise characteristics may be a consequence of (1) widespread vocal plasticity, where most individuals have the ability to adjust song as needed, (2) heritable differences in singing that result from selective pressures related to signal transmission in loud environments, (3) differences during critical song-learning periods, such that nestlings in louder environments develop different song characteristics, (4) ecological differences among environments that affect individual conditions in ways that ultimately also affect singing behavior, and (5) different social interactions in urban areas result from different population densities, pairing status, levels of competition, and/or predation risk.

The possibility that noise-associated shifts in song characteristics could be attributed to behavioral differences mediated by genes or active learning is particularly interesting. Others have suggested that genetic shifts may underlie song differences between rural and urban populations (Partecke 2004, Partecke 2006). If urban environments select for higher frequency songs, then populations in loud environments could conceivably diverge from those in more quiet locations in cases where song frequency influences success in mate attraction and territory defense (Ellers and Slabbekoorn 2003, Podos et al. 2004, Slabbekoorn and van Boer-Visser 2006, Slabbekoorn and Smith 2002b). Song divergence could also result during the sensitive phase of young passerines. Songbirds acquire their songs by copying those of other males, and the low-frequency components of songs might not be transmitted effectively through urban noise to be learned in noisy environments, possibly leading birds to sing with higher minimum frequencies (Hansen 1979). These higher frequencies would be heard more often by young birds, therefore disproportionately represented in their songs (Podos et al. 2004). Should loud ambient noise make it difficult females to hear low-frequency songs and therefore not respond to the males singing these lower songs, the males (during their song crystallization process) may increase usage of high-frequency songs to attract females. These high-frequency songs would then be retained upon the denouement of crystallization and the low-frequency songs would be lost in the attenuation process. One further mechanism might be the regulation of song frequencies by the individual itself, such that a bird alters the minimum frequency of a given song if immediately previous songs are masked by the concurrent ambient noise (Brumm and Todt 2003, Slabbekoorn and van Boer-Visser, 2006).

Although my findings are consistent with expected shifts in song characteristics of urban acoustic environments, this study has a number of limitations that must be noted. First, despite my efforts to reduce extraneous sources of variation (e.g. recording location, habitat, and weather) from my study, there were some differences in location, habitat, and weather among the acoustic environments. Consequently, the possibility exists that the acoustic environments differed in the resources that they offered to birds and these resources (not the noise levels) ultimately affected singing behavior. For example, nutritional supplements (i.e. bird feeders) might alter singing behavior through the improvement of immunocompetence and assured less foraging time (Podos et al. 2004). I did not survey sources of additional food resources or evaluate the health of recorded birds to determine whether nutritional benefits had any effect on singing behavior. Second, differences in pairing status and/or nesting stage can affect singing behavior (De Ridder et al. 2004), but these were not directly assessed. Third, due to factory preset parameters of the Marantz's recording of songs in MP3 format with 32 kbps bitrate, the highest frequencies of cardinal song in highway acoustic environments may have been digitally discriminated against and not recorded. However, this potential bias should result in a more conservative test and would be expected to only reinforce the positive association between frequency and ambient noise.

Despite these shortcomings, my findings illustrate the importance of understanding subtle behavioral consequences of urbanization. While I did not examine reproductive consequences of different song characteristics, previous research has demonstrated that song characteristics can profoundly affect territory defense, mate acquisition, and other social interactions that can ultimately influence individual fitness (Badyaev and Leaf 1997). In addition, some species may not settle in loud environments altogether (Finch and Hawksworth 2006). Thus, increasing levels of noise pollution surrounding natural areas and reserves has the potential to reduce the quality of their bird conservation efforts. Future research is needed to focus on a wider array of bird species in order to understand how entire avian communities respond to changing acoustic environments. Other helpful research would include experimental tests for differences in signal transmission among a variety of acoustic environments. These tests would need to identify the extent that transmission differences result directly from masking by either loud noises or by less effective transmission through habitat modifications such as foliage volume fluctuations or created echoing through buildings.

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Variable	Highway	Commercial	Residential	Rural	F	P
Low frequency	1725.9(30.4)	1740.4(29.8)	1602.8(34.7)	1542.6(31.4)	9.62	<.0001
High frequency	5181.5(229.3)	4918.0(302.5)	5796.9(147.0)	5019.7(203.2)	2.40	0.0793
Frequency range	3455.6(238.0)	3177.7(318.0)	4194.1(143.0)	3477.2(206.0)	2.66	0.0587
Max frequency	2875.4(43.6)	2756.6(67.6)	2870.1(43.4)	2838.0(42.4)	1.07	0.3713
Length (sec)	2.2(0.2)	2.6(0.2)	2.3(0.2)	2.6(0.19)	1.27	0.2951
Song rate	6.9(0.7)	6.1(0.4)	5.2(0.5)	7.2(0.62)	2.04	0.1208
cv low freq	0.07(0.01)	0.06(0.01)	0.07(0.01)	0.09(0.01)	3.01	0.0388
cv high freq	0.14(0.02)	0.12(0.02)	0.10(0.02)	0.13(0.01)	0.86	0.4696
cv freq range	0.23(0.03)	0.19(0.03)	0.15(0.03)	0.21(0.01)	1.62	0.1970

Table 1. Song characteristics of 53 American Robins recorded in four acoustic environments in central Ohio 2006.

Variable	Highway	Commercial	Residential	Rural	F	P
Low frequency	1387.7(68.5)	1342.6(36.7)	1299.0(51.0)	1209.4(54.2)	1.42	0.2524
High frequency	6082.1(369.1)	5993.6(296.4)	4986.7(302.2)	5025.1(423.5)	3.55	0.0234
Frequency range	4798.3(274.9)	4651.0(293.8)	3687.7(319.9)	3815.7(468.0)	2.69	0.0601
Max frequency	3103.7(207.7)	3016.4(156.9)	2902.6(108.5)	2788.7(99.4)	0.47	0.7027
Length (sec)	2.8(0.2)	3.3(0.2)	3.1(0.2)	3.0(0.2)	0.50	0.6879
Song rate	10.9(1.11)	10.5(1.2)	10.8(0.6)	8.1(0.7)	2.12	0.1146
Cv low freq	0.10(0.03)	0.08(0.01)	0.11(0.01)	0.11(0.02)	0.86	0.4718
Cv high freq	0.03(0.02)	0.04(0.02)	0.06(0.02)	0.09(0.02)	1.67	0.1894
Cv delta freq	0.06(0.02)	0.07(0.02)	0.10(0.02)	0.15(0.03)	2.56	0.0695

Table 2. Song characteristics of 42 Northern Cardinals recorded in four acoustic environments in central Ohio, 2006.

Variable	Highway	Commercial	Residential	Rural	F	P
% cover by deciduous trees	10.1(3.68)	12.6(3.56)	13.9(4.18)	11.7(2.76)	0.20	0.8967
% cover by conifers	6.3(4.31)	2.4(1.02)	0.9(0.44)	0.8(0.27)	1.31	0.2804
% cover by snags	0.4(0.36)	0.6(0.47)	0.3(0.36)	0.2(0.09)	0.40	0.7513
% cover by shrubs & saplings	8.4(2.87)	14.2(5.78)	3.7(1.08)	6.2(3.20)	1.34	0.2724
% cover by herb. Vegetation	29.6(8.39)	12.3(5.22)	5.6(3.51)	45.6(5.50)	2.46	0.0738
% cover by lawn	39.4(8.26)	16.5(6.84)	28.8(6.32)	16.4(3.83)	3.44	0.0237
% cover by pavement	26.1(1.85)	22.2(8.48)	41.8(5.36)	16.4(3.83)	3.37	0.0255
Number of buildings	0.1(0.10)	1.4(0.28)	1.7(0.36)	0.7(0.21)	8.10	0.0002
Canopy height (m)	12.6(1.84)	13.5(0.99)	14.3(0.51)	12.8(1.63)	0.24	0.8664

Table 3. Differences in habitat characteristics recorded within a 25 m radius circular plot surrounding location of 53 American Robins in four acoustic environments in central Ohio, 2006

Variable	**Highway**	**Commercial**	**Residential**	**Rural**	**F**	**P**
% cover by deciduous trees	25.2(10.5)	20.7(5.52)	25.4(5.29)	22.6(6.76)	0.12	0.9475
% cover by conifers	1.7(1.66)	0.4(0.16)	0.9(0.58)	0.8(0.62)	0.39	0.7631
% cover by snags	0.3(0.21)	1.8(1.00)	0.4(0.17)	0.8(0.37)	1.61	0.2041
% cover by shrubs & saplings	12.0(6.29)	16.7(5.20)	24.0(6.42)	32.3(13.96)	0.86	0.4723
% cover by herb. Vegetation	20.0(11.25)	18.1(7.55)	12.5(5.98)	13.1(4.99)	0.24	0.8687
% cover by lawn	33.3(15.20)	20.5(8.31)	30.7(7.77)	36.3(10.85)	0.44	0.7273
% cover by pavement	20.0(15.33)	10.5(5.80)	15.1(4.67)	11.9(4.62)	0.32	0.8140
Number of buildings	0.5(0.34)	0.6(0.22)	0.7(0.19)	0.8(0.31)	0.16	0.9251
Canopy height (m)	15.0(3.42)	17.0(1.70)	15.2(1.21)	13.8(1.57)	0.53	0.6676

Table 4. Differences in habitat characteristics recorded within a 25 m radius circular plot surrounding location of 42 Northern Cardinals in four acoustic environments in central Ohio, 2006.

Variable	**Highway**	**Commercial**	**Residential**	**Rural**	**F**	**P**
Bird to mic horizontal (m)	5.9(1.55)	6.6(2.11)	5.9(1.51)	7.9(1.53)	0.36	0.7788
Bird to mic vertical (m)	10.5(1.21)	12.5(1.35)	13.0(0.10)	11.5(1.01)	0.87	0.4633
Cloud cover	2.5(0.42)	3.5(0.39)	2.2(0.40)	1.6(0.28)	4.34	0.0086
Bird to Road (m)	125.9(20.65)	53.8(12.7)	20.3(6.71)	58.1(1.66)	10.74	<.0001
Temperature	54.4(2.27)	61.0(2.54)	55.1(2.10)	58.1(1.66)	2.41	0.0779
No. of conspecifics	2.2(0.79)	2.6(0.62)	2.1(0.56)	3.3(0.75)	1.57	0.2139
% relative humidity	84.4(2.28)	76.5(3.17)	84.5(2.83)	79.0(2.18)	2.59	0.0631

Table 5. Differences in recording distances and weather conditions where data was measured immediately after the song recording for 53 American Robins in four acoustic environments in central Ohio, 2006.

Variable	Highway	Commercial	Residential	Rural	F	P
Bird to mic horizontal (m)	7.3(2.20)	9.9(2.38)	9.8(1.69)	7.6(1.91)	0.38	0.7707
Bird to mic vertical (m)	11.9(1.83)	15.0(1.75)	13.9(1.11)	13.0(1.25)	0.66	0.5804
Cloud cover	2.5(0.67)	2.1(0.48)	2.6(0.34)	1.5(0.38)	0.44	0.7258
Bird to Road (m)	155.0(30.41)	74.0(18.75)	34.7(8.75)	61.6(17.37)	8.25	0.0002
Temperature	63.2(3.53)	61.0(1.83)	59.2(2.75)	55.6(3.31)	0.83	0.4871
No. of conspecifics	2.0(0.22)	2.4(0.37)	2.6(0.34)	1.5(0.38)	0.67	0.5731
% relative humidity	75.3(4.58)	85.8(1.63)	78.9(2.31	85.6(1.88)	3.25	0.0325

Table 6. Differences in recording distances and weather conditions where data was measured immediately after the song recording for 42 Northern Cardinals in four acoustic environments in central Ohio, 2006.

ID number	Species	Environment	Max freq with background noise	Max freq minus background noise
1014	Noca	Highway	3962.1	3876.0
1025	Amro	Highway	2842.4	2842.4
1031	Amro	Rural	3273.0	3273.0
1036	Noca	Residential	2789.8	2789.8
1050	Amro	Rural	2756.2	2756.2
1060	Amro	Highway	2497.9	2497.9
1075	Amro	Residential	2670.1	2670.1
1083	Amro	Residential	2842.4	2842.4
1116	Amro	Commercial	2756.2	2756.2
1117	Noca	Rural	2411.7	2411.7
1126	Noca	Residential	3876.0	3876.0
1140	Amro	Highway	2756.2	2756.2
1142	Amro	Highway	2153.3	2153.3
1144	Amro	Rural	3014.6	3014.6
1160	Noca	Commercial	3100.8	3100.8
1177	Noca	Highway	3100.8	3100.8
1182	Noca	Residential	2584.0	2584.0
1185	Noca	Residential	4048.2	4048.2
1194	Amro	Commercial	2239.5	2239.5
1195	Amro	Commercial	2411.7	2411.7
1208	Amro	Commercial	2842.4	2842.4
1212	Noca	Commercial	3359.2	3359.2
1213	Amro	Rural	2842.4	2842.4
1222	Noca	Highway	3100.8	3100.8
1224	Noca	Commercial	3703.7	3703.7
1234	Noca	Commercial	3359.2	3359.2
1237	Amro	Residential	2928.5	2928.5
1253	Noca	Rural	2239.5	2239.5
1255	Amro	Rural	3100.8	3100.8
1258	Amro	Rural	3273.0	3273.0
1274	Noca	Commercial	4651.2	4651.2
1282	Amro	Highway	2497.9	2497.9
1306	Noca	Residential	2067.2	2067.2
1314	Amro	Rural	2842.4	2842.4
1328	Amro	Rural	3100.8	3100.8

Table 7. Comparisons of maximum frequencies in randomly selected songs with and without background noise.

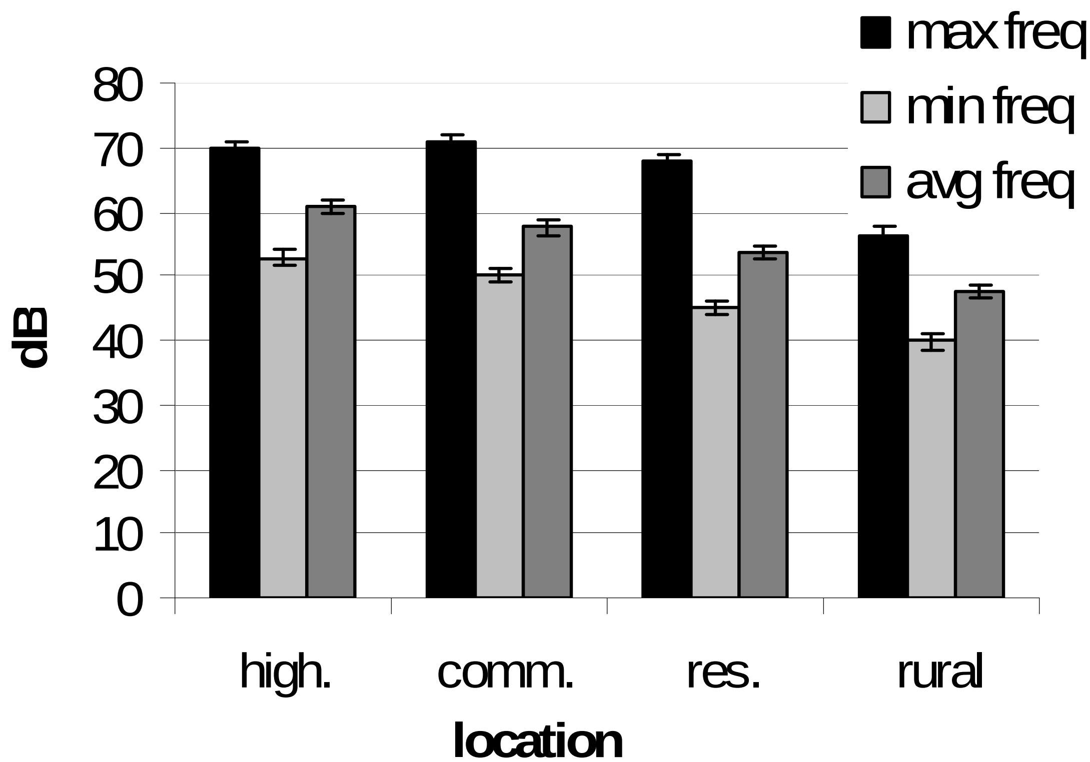

Figure 1. The amount of background noise at each of the four *a priori* acoustic environments in central Ohio, 2006.

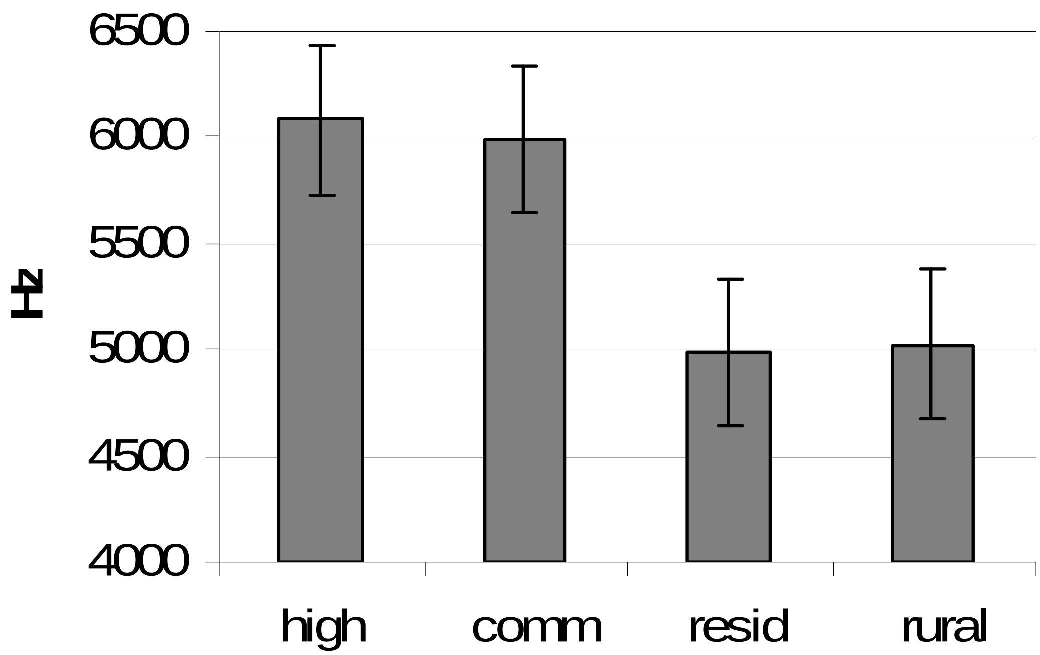

Figure 2. Differences in high frequency notes used in songs in four acoustic environments (highway, commercial, residential, and rural) for 42 Northern Cardinal songs recorded in central Ohio, 2006.

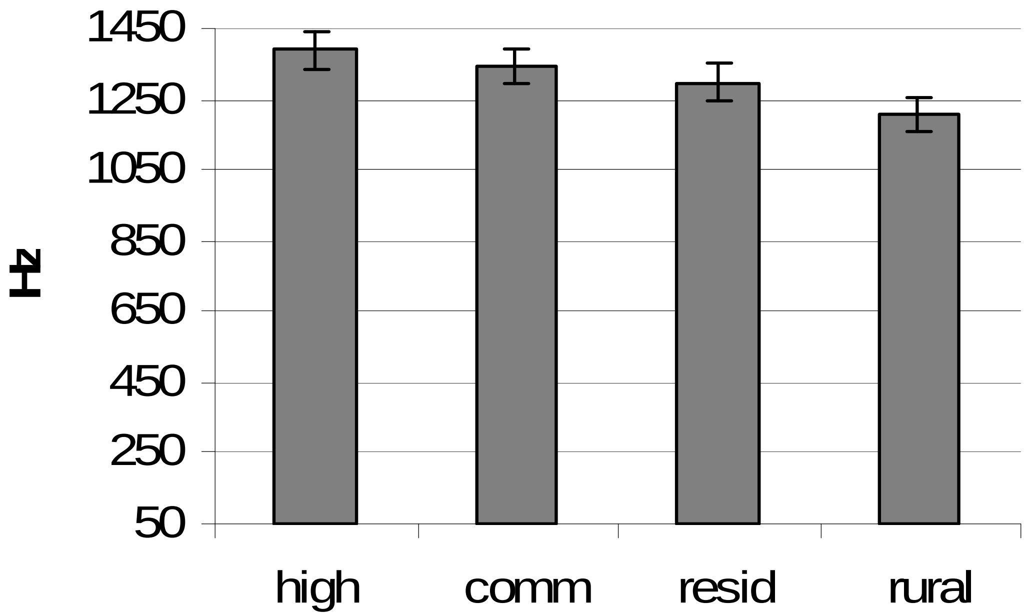

Figure 3. Differences in low frequency notes used in songs in four acoustic environments (highway, commercial, residential, and rural) for 42 Northern Cardinal songs recorded in central Ohio, 2006.

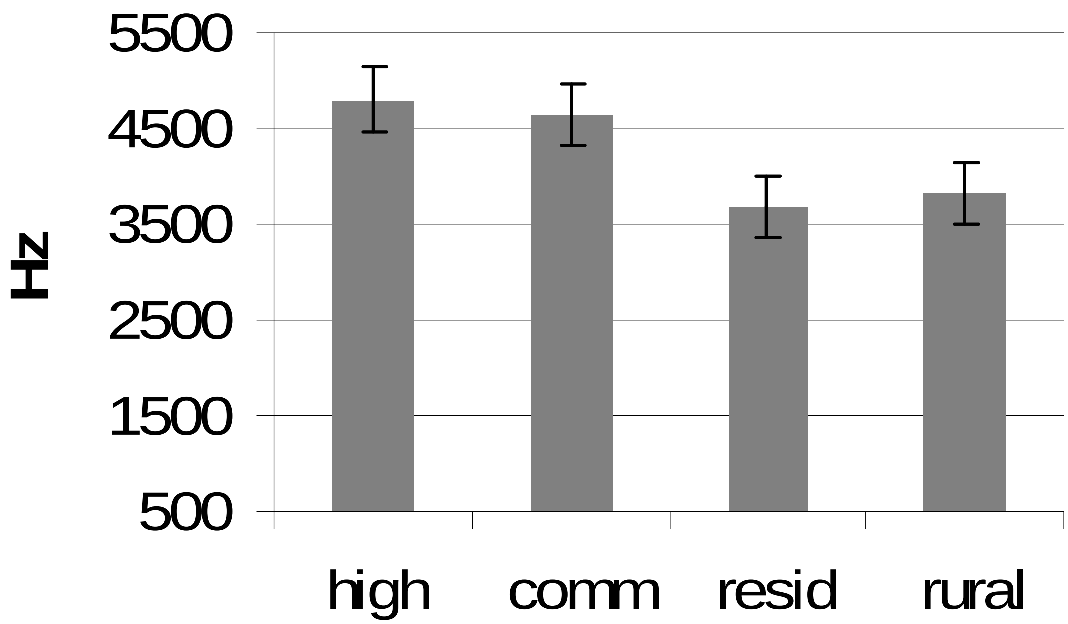

Figure 4. Differences in frequency ranges (high-low frequencies) among four acoustic environments (highway, commercial, residential, and rural) for 42 Northern Cardinal songs recorded in central Ohio, 2006.

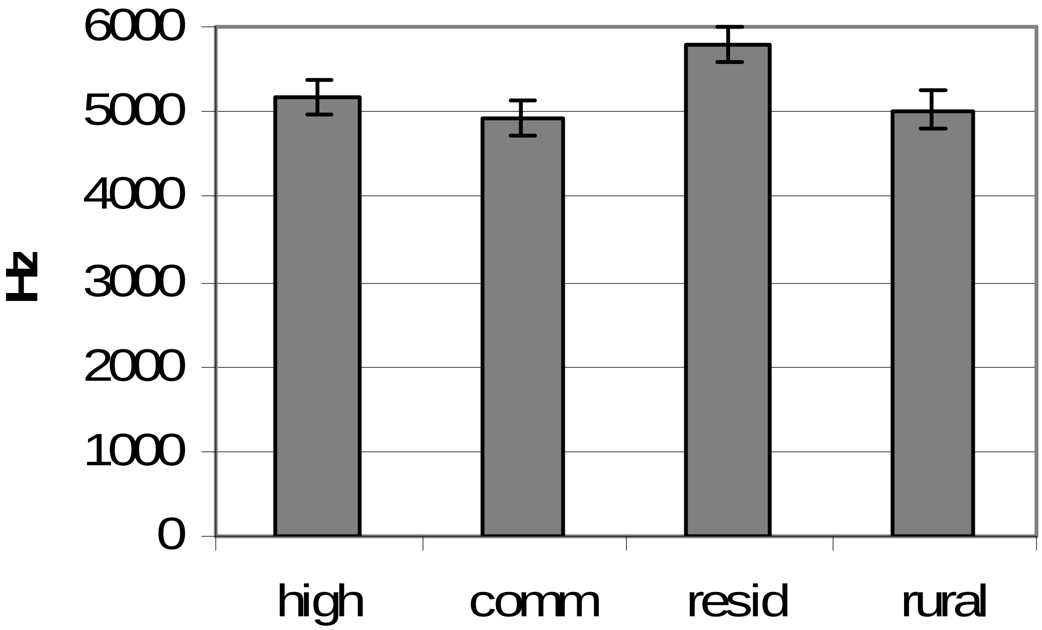

Figure 5. Differences in high frequency notes used in songs in four acoustic environments (highway, commercial, residential, and rural) for 53 American Robin songs recorded in central Ohio, 2006.

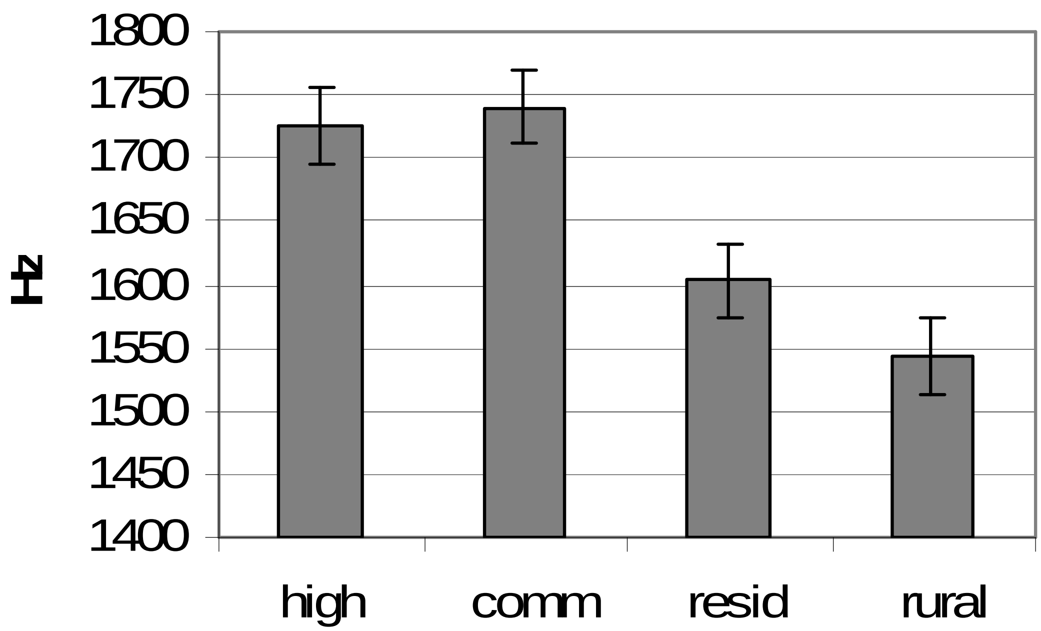

Figure 6. Differences in low frequency notes used in songs in four acoustic environments (highway, commercial, residential, and rural) for 53 American Robin songs recorded in central Ohio, 2006.

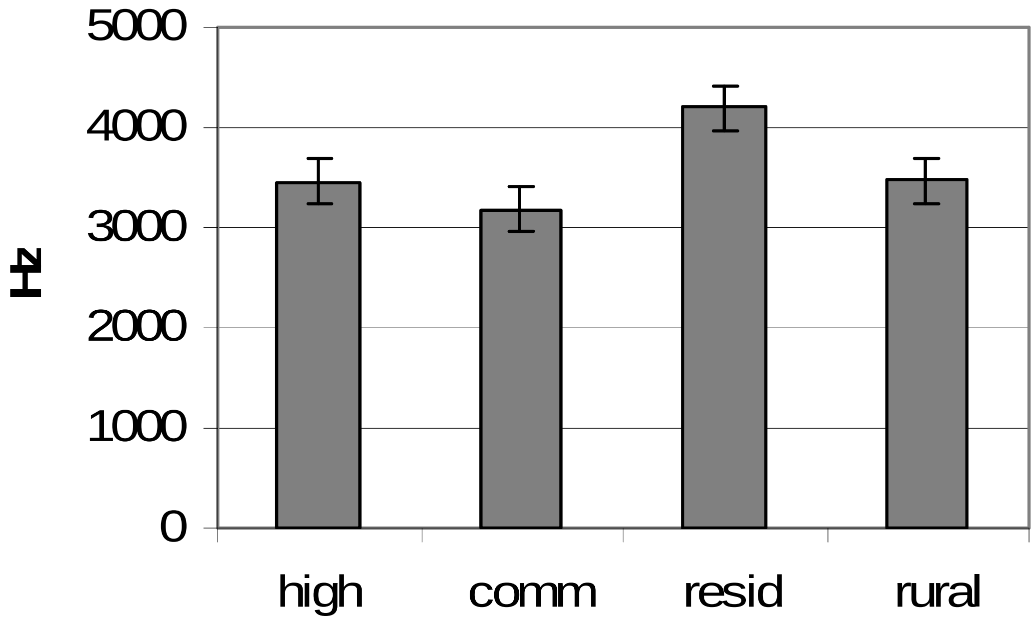

Figure 7. Differences in frequency ranges (high-low frequencies) among four acoustic environments (highway, commercial, residential, and rural) for 53 American Robin songs recorded in central Ohio, 2006.

Appendices

BirdID	Date	Location	Avg highfreq	Avg lowfreq	Avg range	Avg maxfreq
1014	5/2/2006	Highway	1401.6	6500.2	5098.6	2646.4
1021	5/3/2006	Highway	1463.4	6384.6	4921.1	3242.3
1176	5/30/2006	Highway	764.3	4248.3	3484.0	3769.6
1177	5/30/2006	Highway	1421.2	6598.7	5177.5	3359.2
1222	6/8/2006	Highway	1127.0	6464.3	5337.3	3236.1
1329	7/6/2006	Highway	1525.1	6296.3	4771.3	2368.7
1034	5/9/2006	Commercial	1480.3	6477.8	4997.6	2965.5
1160a	5/25/2006	Commercial	1221.2	5827.6	4606.4	2825.1
1160b	5/25/2006	Commercial	1300.0	3510.1	2210.0	2540.9
1202	6/5/2006	Commercial	1427.7	6407.7	4980.0	2344.7
1212	6/6/2006	Commercial	1342.5	6430.7	5088.2	3298.9
1224	6/9/2006	Commercial	1113.2	6541.9	5428.7	3024.2
1231	6/9/2006	Commercial	1477.9	6214.1	4736.2	3136.2
1234	6/9/2006	Commercial	1364.1	5508.8	4144.7	3370.7
1274	6/19/2006	Commercial	1409.6	6531.3	5121.7	4065.5
1276	6/19/2006	Commercial	1289.9	6486.0	5196.1	2592.6
1035	5/10/2006	Residential	1205.9	6522.5	5316.6	2775.0
1036	5/10/2006	Residential	1144.8	6454.8	5310.0	3215.6
1042	5/10/2006	Residential	1097.3	3107.2	2009.8	2469.1
1044	5/10/2006	Residential	1083.2	3435.6	2352.4	2282.5
1080	5/17/2006	Residential	997.1	6501.5	5504.4	3927.6
1120	5/22/2006	Residential	1347.2	6483.9	5136.7	3471.1
1125	5/22/2006	Residential	1339.7	4828.6	3488.9	3467.4
1126	5/22/2006	Residential	1474.6	6157.0	4682.4	2909.4
1129	5/22/2006	Residential	1379.1	4307.1	2927.9	2918.3
1167	5/26/2006	Residential	1715.6	3464.3	1748.7	2575.4
1168	5/26/2006	Residential	1727.5	4437.5	2710.0	3074.7
1172	5/26/2006	Residential	1246.4	4393.7	3147.3	2424.0
1182	5/31/2006	Residential	1454.2	4659.3	3205.1	2596.3
1184	5/31/2006	Residential	1191.3	5564.3	4373.0	2747.6
1186	5/31/2006	Residential	1358.1	4527.7	3169.6	2868.6
1192	5/31/2006	Residential	1068.9	6444.2	5375.3	3209.9
1306	6/27/2006	Residential	1252.1	3484.5	2232.4	2411.7

1052	5/15/2006	Rural	903.3	6445.7	5542.4	2331.0
1056	5/15/2006	Rural	1125.9	6324.0	5198.1	3322.9
1117	5/19/2006	Rural	1137.8	5659.7	4521.9	2778.9
1253	6/14/2006	Rural	1147.6	5508.3	4360.7	3034.5
1305	6/27/2006	Rural	1254.6	3598.1	2343.5	2597.2
1307b	6/28/2006	Rural	1400.6	3496.9	2096.3	2709.9
1322a	6/29/2006	Rural	1153.2	6042.1	4888.9	2786.2
1323	6/29/2006	Rural	1403.1	4900.5	3497.4	3005.1
1325	6/30/2006	Rural	1358.8	3250.6	1891.7	2532.3

Table 8. Song characteristics and recording dates for 42 individual Northern Cardinals recorded in central Ohio, 2006.

BirdID	Date	Location	Avg highfreq	Avg lowfreq	Avg range	Avg maxfreq
1018	5/3/2006	Highway	1756.3	5490.6	3734.4	3068.0
1025	5/5/2006	Highway	1617.5	6098.6	4481.1	2788.6
1049	5/12/2006	Highway	1581.6	4229.0	2647.4	3077.0
1060	5/16/2006	Highway	1744.5	5165.9	3421.3	2960.8
1063	5/16/2006	Highway	1818.2	6433.7	4615.4	3146.5
1065	5/16/2006	Highway	1826.4	5243.8	3417.5	2965.4
1140	5/23/2006	Highway	1716.8	3854.6	2137.9	2776.1
1142	5/23/2006	Highway	1872.1	4499.1	2627.0	2675.2
1221	6/8/2006	Highway	1630.1	4743.8	3113.7	2928.5
1244	6/13/2006	Highway	1805.4	4116.5	2311.1	2696.6
1278	6/20/2006	Highway	1585.0	5450.0	3865.0	2845.1
1280	6/20/2006	Highway	1932.3	4705.1	2772.8	2938.4
1282	6/20/2006	Highway	1655.2	6259.9	4604.7	2601.2
1284	6/20/2006	Highway	1621.2	6250.4	4629.2	2788.0
1032	5/9/2006	Commercial	1578.4	5270.1	3691.8	2862.5
1116	5/18/2006	Commercial	1622.6	4753.8	3131.3	2627.1
1194	6/2/2006	Commercial	1894.9	3641.9	1746.9	2373.5
1195	6/2/2006	Commercial	1783.9	3610.9	1827.0	2497.9
1208	6/6/2006	Commercial	1697.0	5107.0	3410.1	2660.9
1285	6/22/2006	Commercial	1754.8	4021.4	2266.6	2876.8
1293	6/23/2006	Commercial	1764.1	5459.7	3695.6	2612.7
1294	6/23/2006	Commercial	1895.2	3986.5	2091.3	2971.6
1295	6/23/2006	Commercial	1670.5	5510.2	3839.7	2741.3
1296	6/26/2006	Commercial	1728.0	6267.0	4539.0	3057.7
1297	6/26/2006	Commercial	1754.7	6469.8	4715.1	3040.8
1039	5/10/2006	Residential	1606.1	5898.7	4292.6	2854.3
1075	5/17/2006	Residential	1639.8	5252.1	3612.3	2768.0
1077	5/17/2006	Residential	1314.1	5328.2	4014.1	2709.6
1083	5/17/2006	Residential	1544.8	6341.9	4797.1	2970.1
1170	5/26/2006	Residential	2903.7	8782.4	5878.8	2513.5
1196	6/5/2006	Residential	1681.2	5945.2	4263.9	2835.2
1237	6/12/2006	Residential	1641.7	5223.5	3581.8	2695.4
1238	6/12/2006	Residential	1632.3	6414.2	4781.9	2978.2
1239	6/12/2006	Residential	1670.5	6352.7	4682.2	3121.6
1286	6/22/2006	Residential	1612.4	5672.3	4059.9	2973.8
1292	6/22/2006	Residential	1685.3	5540.6	3855.3	2795.4
1031	5/8/2006	Rural	1744.9	6295.5	4550.7	3051.2
1050	5/15/2006	Rural	1692.8	3889.7	2196.9	2787.6
1144	5/24/2006	Rural	1648.0	4112.7	2464.7	2837.4

1213	6/7/2006	Rural	1528.7	5520.0	3991.3	3031.9
1215	6/7/2006	Rural	1654.8	6054.3	4399.4	2693.8
1220	6/9/2006	Rural	1380.8	4016.9	2636.1	2842.4
1255	6/14/2006	Rural	1574.3	5897.0	4322.7	2955.0
1258	6/14/2006	Rural	1607.2	4065.8	2458.7	2856.7
1260	6/14/2006	Rural	1406.2	6264.8	4858.7	2875.5
1261	6/16/2006	Rural	1696.1	5500.2	3804.1	2885.4
1267	6/16/2006	Rural	1411.1	5778.9	4367.8	3211.5
1270	6/16/2006	Rural	1528.0	5616.6	4088.7	2706.0
1307a	6/28/2006	Rural	1599.9	3984.2	2384.3	2898.4
1314	6/28/2006	Rural	1294.3	4963.6	3669.2	2878.3
1315	6/28/2006	Rural	1340.2	4664.6	3324.4	2537.6
1318	6/29/2006	Rural	1652.9	4097.8	2444.9	2461.0
1324	6/30/2006	Rural	1540.7	4941.5	3400.8	2670.1
1328	6/30/2006	Rural	1465.0	4690.3	3225.3	2904.6

Table 9. Song characteristics and recording locations for 53 individual American Robins recorded in central Ohio, 2006.

BirdID	Date	Location	Total time (sec)	Song rate (songs/sec)	Avg song length (sec)
1014	5/2/2006	Highway	228.6	13.45	3.57
1021	5/3/2006	Highway	193.8	13.8	3.37
1176	5/30/2006	Highway	343.5	10.10	2.82
1177	5/30/2006	Highway	118.1	7.38	2.61
1222	6/8/2006	Highway	197.4	12.34	3.39
1329	7/6/2006	Highway	100.2	8.35	2.25
1034	5/9/2006	Commercial	129.0	9.21	4.82
1160a	5/25/2006	Commercial	221.8	11.67	3.49
1160b	5/25/2006	Commercial	110.8	7.91	2.93
1202	6/5/2006	Commercial	315.4	17.52	3.08
1212	6/6/2006	Commercial	78.4	7.84	2.68
1224	6/9/2006	Commercial	87.9	9.77	4.00
1231	6/9/2006	Commercial	123.0	7.24	2.82
1234	6/9/2006	Commercial	284.8	16.75	2.95
1274	6/19/2006	Commercial	174.6	8.73	3.09
1276	6/19/2006	Commercial	90.7	8.25	3.09
1035	5/10/2006	Residential	236.3	10.28	3.12
1036	5/10/2006	Residential	46.1	7.69	3.12
1042	5/10/2006	Residential	140.7	11.73	2.92
1044	5/10/2006	Residential	124.6	12.46	4.60
1080	5/17/2006	Residential	56.5	11.30	4.33
1120	5/22/2006	Residential	118.8	11.88	2.74
1125	5/22/2006	Residential	398.2	10.21	3.58
1126	5/22/2006	Residential	148.6	7.08	1.68
1129	5/22/2006	Residential	676.4	16.10	2.84
1167	5/26/2006	Residential	97.3	9.73	1.47
1168	5/26/2006	Residential	253.8	7.69	1.98
1172	5/26/2006	Residential	185.9	13.28	3.47
1182	5/31/2006	Residential	120.8	8.63	3.44
1184	5/31/2006	Residential	148.3	14.83	3.23
1186	5/31/2006	Residential	176.6	7.68	2.89
1192	5/31/2006	Residential	179.6	11.97	3.70
1306	6/27/2006	Residential	123.8	10.31	2.76
1052	5/15/2006	Rural	308.0	9.63	3.85
1056	5/15/2006	Rural	119.9	6.31	3.33
1117	5/19/2006	Rural	169.1	8.90	2.87
1253	6/14/2006	Rural	87.3	6.72	2.61
1305	6/27/2006	Rural	101.9	7.84	3.09
1307b	6/28/2006	Rural	264.0	12.00	2.56

1322a	6/29/2006	Rural	192.3	8.74	4.16
1323	6/29/2006	Rural	75.2	6.26	2.90
1325	6/30/2006	Rural	60.9	6.09	2.06

Table 10. Song length and song rate for 42 individual Northern Cardinals recorded in central Ohio, 2006.

BirdID	Date	Location	Total time (sec)	Song rate (songs/sec)	Avg song length (sec)
1018	5/3/2006	Highway	213.9	5.22	2.04
1025	5/5/2006	Highway	674.0	14.04	2.02
1049	5/12/2006	Highway	209.4	7.22	3.25
1060	5/16/2006	Highway	125.9	5.72	1.42
1063	5/16/2006	Highway	212.7	4.34	1.49
1065	5/16/2006	Highway	153.0	5.46	1.57
1140	5/23/2006	Highway	129.2	9.94	2.36
1142	5/23/2006	Highway	91.6	5.09	1.54
1221	6/8/2006	Highway	199.9	7.14	2.28
1244	6/13/2006	Highway	69.8	4.65	1.88
1278	6/20/2006	Highway	255.2	7.98	1.76
1280	6/20/2006	Highway	163.78	5.28	1.54
1282	6/20/2006	Highway	108.5	7.23	3.31
1284	6/20/2006	Highway	137.3	7.23	3.77
1032	5/9/2006	Commercial	159.3	5.31	4.35
1116	5/18/2006	Commercial	155.4	5.55	2.79
1194	6/2/2006	Commercial	242.5	7.58	2.72
1195	6/2/2006	Commercial	112.0	4.87	2.01
1208	6/6/2006	Commercial	162.1	5.79	2.79
1285	6/22/2006	Commercial	265.7	8.86	2.06
1293	6/23/2006	Commercial	216.4	5.69	2.34
1294	6/23/2006	Commercial	75.4	6.29	3.66
1295	6/23/2006	Commercial	118.5	5.15	2.09
1296	6/26/2006	Commercial	67.8	5.65	1.90
1297	6/26/2006	Commercial	134.2	5.84	2.39
1039	5/10/2006	Residential	148.0	5.10	1.90
1075	5/17/2006	Residential	94.7	4.12	1.66
1077	5/17/2006	Residential	117.9	4.21	2.00
1083	5/17/2006	Residential	176.9	6.10	3.22
1170	5/26/2006	Residential	81.3	3.70	1.35
1196	6/5/2006	Residential	86.9	5.11	1.39
1237	6/12/2006	Residential	80.2	4.72	2.35
1238	6/12/2006	Residential	92.6	2.89	2.00
1239	6/12/2006	Residential	282.6	8.56	3.58
1286	6/22/2006	Residential	115.0	6.05	2.16
1292	6/22/2006	Residential	116.6	5.30	2.42
1031	5/8/2006	Rural	234.6	7.11	2.52
1050	5/15/2006	Rural	130.8	3.96	1.61
1144	5/24/2006	Rural	131.2	3.75	1.43

1213	6/7/2006	Rural	225.4	9.39	2.46
1215	6/7/2006	Rural	274.7	6.87	2.09
1220	6/9/2006	Rural	122.8	8.18	4.47
1255	6/14/2006	Rural	125.5	4.83	2.43
1258	6/14/2006	Rural	88.0	7.34	1.77
1260	6/14/2006	Rural	98.9	7.61	2.60
1261	6/16/2006	Rural	188.1	3.92	1.89
1267	6/16/2006	Rural	131.8	9.42	3.55
1270	6/16/2006	Rural	104.2	6.95	3.67
1307a	6/28/2006	Rural	339.0	14.74	1.79
1314	6/28/2006	Rural	68.8	5.73	2.92
1315	6/28/2006	Rural	76.6	5.89	3.21
1318	6/29/2006	Rural	83.9	5.99	2.77
1324	6/30/2006	Rural	148.7	9.29	2.22
1328	6/30/2006	Rural	156.3	8.69	3.04

Table 11. Song rate and song length for 53 individual American Robins recorded in central Ohio, 2006.